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Testing predictions of stream landscape theory for fish assemblages in highly fragmented watersheds

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Abstract. Predictions of stream landscape theory were tested with common agency fishery data in watersheds heavily fragmented by dams and barriers; large stream fragments support higher species diversity, more abundant populations, and a greater range of fish sizes. Study watersheds discharge to the Hudson River in New York USA, drain rocky and high relief landscapes, and have numerous mill dams and stream barriers. Stream fragments with fish collections ranged from 0.3 km to 119 km in contiguous length. Larger stream fragments had more diverse fish communities but not higher fish densities nor a wider range of fish sizes. However, almost all large stream fragments were supporting reproduction and rearing of the dominant stream species (brown trout *Salmo trutta*, brook trout *Salvelinus fontinalis*) while small fragments had no evidence of providing this fish community support. Therefore, consistent with the fundamental basis of stream landscape theory, large stream networks provide support for more species and more secure populations. The study supports the concept that diverse fish communities and secure populations benefit from access to a wide range of stream habitats.

Key words: stream connections, fish communities, Salmonidae, fish barriers, aquatic landscapes, fragmentation

Introduction

The disruption of habitat connections, or fragmentation, has been regarded as an important threat to biodiversity and population security (Wilcove et al. 1998, Ward et al. 1999, Fagan et al. 2002). Also, the free movement of individuals across landscapes promotes the persistence of local animal populations through time (Campbell Grant et al. 2007). The size of habitat fragments (e.g., Lesinski et al. 2007) and barriers to animal movement (e.g., Taylor et al. 1993, Rico et al. 2007) have been shown to be important for conservation of communities in terrestrial landscapes. Fragmentation of riverine landscapes has also been regarded as a serious threat to native fish faunas (Letcher et al. 2007, Raeymaekers et al. 2009). Currently there are many efforts across Europe to re-establish river and stream connections to meet the waterway standard of good ecological status under the European Union's Water Framework Directive.

The impact of dams and barriers on the movement of anadromous fish has been well recognized since

the onset of the industrial revolution in Europe and North America when water mills, barge canals, and stream diversions became common in high relief terrain. However, the detrimental effects of stream fragmentation on resident fishes is a much more recent concern for fish conservation and management (Gowan et al. 1994). Study findings accumulating slowly in the last two decades indicate that fish movement plays a critical role in linking different life stages to proper habitats throughout the life cycle (e.g., Valová et al. 2006). This concept, sometimes called stream landscape theory or the riverscape concept (Ward 1998, Fausch et al. 2002), has been growing in importance for protecting and restoring fish biodiversity in rivers and streams. The same concepts were raised earlier (Merriam 1984, Dunning et al. 1992) for terrestrial landscapes. The removal of obsolete dams, diversions, and other barriers has become a common conservation strategy for flowing waters although most attention remains on barriers to anadromous fishes.

Small stream fragments commonly offer a restricted

range of habitats, lack interactions of species and life stages across aquatic landscapes, and limit ecosystem connectivity believed important for maintaining species diversity (Ward 1998, Fausch et al. 2002). A range of habitats are needed to complete many fish life histories (Schlosser 1991), and population dynamics are influenced by the availability of appropriate habitats under varying environmental conditions (Schlosser 1995, Harig & Fausch 2002). Findings on fish populations in small, isolated stream fragments has revealed local populations with shorter generation time and a dominance of younger and smaller fish (Letcher et al. 2007). Finally, larger fish often require seasonal availability of deep habitats (Harig & Fausch 2002) and fish movement can redistribute the range of fish sizes across a watershed (Riley et al. 1992). From these findings on stream landscapes, we believe that allowing free fish movement across large stream fragments can result in more diverse, larger, and better secured populations with a greater range of fish sizes. The purpose of this study was to test key elements of stream landscape theory in highly fragmented watersheds where fish fauna restoration by barrier removal is being considered by the state government. We also evaluate the feasibility of testing stream landscape theory predictions using large scale and long term data developed in government fishery and watershed restoration programs. Our specific objectives were to (1) test the predictions of stream landscape theory that fish species diversity, fish abundance, and the range of fish sizes is positively related to stream fragment size, and (2) to determine if watershed scale and historical fishery data can be used to test these predictions.

Material and Methods

Our study was conducted using New York Department of Environmental Conservation (NYDEC) data sets and information on two tributary watersheds of the Hudson River, USA. The agency has conducted a variety of studies in these watersheds for planning environmental conservation activities. The watersheds are about 88 km upriver from New York City, drain rocky and high relief landscapes, and were developed early in the European colonization of North America. Moodna Creek discharges (7.35 m³/s; estimated mean flow) to the Hudson River from the West at 41° 27.249' N and 74° 1.097' W. The Moodna Creek watershed has a surface area of 468 km² with mixed land covers: 61% forest and wetlands, 20% agriculture, and 17% developed (Mickelson 2008). There are 382 km of streams in the watershed and as many as 282 dams (Whyte 2006) for an estimated average

stream fragment (barrier bracketed reach) length of 1.35 km. On detailed investigation many dams and stream obstructions no longer posed a barrier to fish movements. Eleven isolated stream fragments were identified with recent NYDEC surveys of stream barriers that also had fish collections in the NYDEC Bureau of Fisheries database.

Fishkill Creek and three small adjacent tributaries drain the East side of the Hudson River and are very similar to Moodna Creek. Land cover was also similar: 59% forest and wetlands, 11% agriculture, and 21% developed (Burns et al. 2005). The Fishkill Creek watershed (500 km²; Burns et al. 2005) contributes 7.85 m³/s (estimated mean flow using 21 years of stream gage data of the US Geological Survey, USGS) to the Hudson River at 41° 29.184' N, 73° 58.662' W. There are 544 km of streams in the basin and at least 350 dams (Burns et al. 2005) making the mean stream fragment size approximately 1.55 km. As in the Moodna Creek watershed, upon investigation many dams and stream obstructions showed they no longer posed a barrier to fish movements. Using confirmed stream fragments, 20 had one or more stream fish surveys in the NYDEC Bureau of Fisheries database. The NYDEC developed distributional analyses of dams and barriers in the study watersheds. Potential dams were located by visually scanning stream channels using aerial photographs (0.19 m per pixel true color orthoimages, 0.30 m per pixel infrared orthoimagery, New York statewide digital orthoimagery). Most identified dams were then field verified in 2005 by NYDEC and for some streams by trained volunteers with photography and standardized field notes. However, the NYDEC investigators do not believe the dam distribution surveys were free of errors. Geographic information system (GIS) coverages were developed from the ground-truthed orthoimages using Arc GIS 9.0. All digitizing was done at a 1:2000 scale by the same NYDEC analysts who completed the field surveys. A review of the development of the dam distribution data were reported by Sayles (2005) and Whyte (2006) and we obtained the resulting GIS files. The editor tool in ArcGIS 9.3 was used to split, merge and measure the length of stream sections between barriers. We included all stream channels in tributaries as part of each fragment length. Impounded surface water was subtracted from stream fragment lengths. Stream fragments with direct connections to the Hudson River and presence of marine and estuarine fish were deleted. We detected some errors in the GIS files and carefully inspected surface water shape files, digital elevation data, and Google Earth imagery to

make corrections. Finally, we used only fragments that had NYDEC fish surveys included since we required both fragment lengths and fish survey data. For each fragment used, the downstream elevations (m above sea level) of the stream or impoundment surface were estimated from USGS digital elevation models and checked with digital topographic maps.

Fish survey data were obtained from the NYDEC Bureau of Fisheries. The collections were completed from the mid-1970s to 2006 and varied in their purpose and fish recording practices. Electrofishing was the routine sampling method. Some surveys recorded all fish greater than about 40 mm total length and others focused on trout but listed other species (species names in Table 1). Notes were included on sampling purpose, wild and stocked source of captured trout, location, and methods. We considered each sampling report as one collection and did not further define effort

or effectiveness because reporting differed in details.

When a final data set of stream fragment lengths and fish collections was assembled, statistical analyses were conducted by first inspecting the distribution of each variable. Stream fragment length and fish densities (counts per sample) were highly skewed and LOG_{10} transformed to centralize the distribution mode. Fish length variables (total length in mm; average, standard deviation, minimum, maximum, and length range) were fairly concentrated in the middle of the distribution range so no transformations were applied. The number of fish species recorded in each stream fragment and the minimum elevation of the fragment were also centrally concentrated thus no transformation was applied. Pairwise scatterplots and regression analyses were conducted for each variable and fragment length to test stream landscape theory predictions. Elevations were also included in

Table 1. North American common names and scientific names of all fish species in the collections used in the study with descriptive statistics on total lengths. The median and interquartile (IQ) range values were used since some distributions were skewed.

| Common and scientific species name | N | Total length (mm) | | |
|--|-----|-------------------|----------|---------|
| | | Median | IQ range | Range |
| Brown trout, <i>Salmo trutta</i> ; stocked | 500 | 257 | 230–281 | 152–394 |
| Brown trout, <i>Salmo trutta</i> ; wild | 359 | 93 | 75–186 | 41–478 |
| Brook trout, <i>Salvelinus fontinalis</i> ; stocked | 14 | 212 | 193–230 | 159–230 |
| Brook trout, <i>Salvelinus fontinalis</i> ; wild | 36 | 123 | 75–160 | 55–224 |
| White sucker, <i>Catostomus commersoni</i> | 50 | 314 | 226–357 | 54–428 |
| Bluegill, <i>Lepomis macrochirus</i> | 30 | 114 | 88–153 | 75–190 |
| Tessellated darter, <i>Etheostoma olmstedti</i> ¹ | 15 | 61 | 61–61 | 57–72 |
| Eastern mudminnow, <i>Umbra pygmaea</i> ¹ | 14 | 66 | 66–66 | 66–66 |
| Creek chub, <i>Semotilus atromaculatus</i> | 13 | 117 | 110–139 | 105–184 |
| Pumpkinseed, <i>Lepomis gibbosus</i> | 13 | 102 | 91–109 | 87–129 |
| Largemouth bass, <i>Micropterus salmoides</i> | 12 | 126 | 93–300 | 70–450 |
| Fallfish, <i>Semotilus corporalis</i> | 7 | 176 | 168–220 | 90–267 |
| Rock bass, <i>Ambloplites rupestris</i> | 7 | 113 | 106–138 | 100–161 |
| Cutlips minnow, <i>Exoglossum maxillingua</i> | 6 | 111 | 59–126 | 57–134 |
| Common shiner, <i>Luxilus cornutus</i> | 6 | 80 | 65–91 | 41–142 |
| Redfin pickerel, <i>Esox americanus</i> | 6 | 171 | 147–188 | 61–230 |
| Redbreast sunfish, <i>Lepomis auritus</i> | 5 | 118 | 100–126 | 95–129 |
| Rainbow trout, <i>Oncorhynchus mykiss</i> ; stocked ¹ | 4 | 342 | 342–342 | 342–342 |
| Smallmouth bass, <i>Micropterus dolomieu</i> | 3 | 266 | | 161–287 |
| Yellow perch, <i>Perca flavescens</i> | 3 | 120 | | 110–134 |
| Brown bullhead, <i>Ameiurus nebulosus</i> | 2 | 318 | | 310–326 |
| Golden shiner, <i>Notemigonus crysoleucas</i> | 2 | 92 | | 88–95 |
| Chain pickerel, <i>Esox niger</i> | 1 | 302 | | |
| Spottail shiner, <i>Notropis hudsonius</i> | 1 | 60 | | |

¹ A relatively large collection of fish at one site had a single length assigned for all individuals.

the regression analyses and correlated with fragment size. The statistical analyses were repeated without fragments and fish collections that had only stocked trout reported. Only the full data set results are reported here because stocked fish are a persistent part of the fish fauna of the study watersheds and results were largely the same. Finally, additional analyses were conducted comparing fragments with and without wild and small young trout (t-test) to determine if trout reproduction and early survival was

linked to stream fragment size and stream elevation. We considered trout smaller than 150 mm total length as wild, stream produced fish because the minimum size of stocked trout has been about 178 mm (NYDEC regional fishery biologist pers. comm.). Trout were also noted as wild or stocked in the NYDEC database.

Results

A total of 31 stream fragments were included in the analyses from the study watersheds. The sampled

Table 2. Data used in the analyses by stream fragment.

| Stream fragment number | Stream fragment length ¹ (km) | Fish species (count) | Fish density ¹ (#/sample) | Total fish length (mm) | | | | Presence of wild young trout ² | Fragment minimum elevation (m) |
|------------------------------|---|----------------------------|--|------------------------|-----|-----|-----|--|---|
| | | | | \bar{X} | SD | max | min | | |
| 1 | 0.4 | 1 | 33 | 264 | 34 | 271 | 112 | 0 | 130 |
| 2 | 0.7 | 3 | 15 | 214 | 57 | 272 | 60 | 0 | 48 |
| 3 | 1.0 | 7 | 45 | 277 | 97 | 428 | 64 | 0 | 76 |
| 4 | 1.1 | 1 | 49 | 257 | 0 | 257 | 257 | 0 | 185 |
| 5 | 1.3 | 1 | 51 | 351 | 0 | 351 | 351 | 0 | 122 |
| 6 | 2.2 | 1 | 22 | 227 | 44 | 287 | 124 | 0 | 113 |
| 7 | 17.9 | 1 | 19 | 155 | 85 | 394 | 46 | 1 | 89 |
| 8 | 4.1 | 4 | 20 | 145 | 67 | 237 | 41 | 1 | 145 |
| 9 | 3.2 | 3 | 26 | 166 | 105 | 450 | 75 | 0 | 55 |
| 10 | 6.7 | 1 | 4 | 195 | 54 | 226 | 116 | 0 | 169 |
| 11 | 8.2 | 2 | 12 | 88 | 13 | 115 | 74 | 1 | 77 |
| 12 | 10.6 | 5 | 18 | 76 | 38 | 168 | 46 | 1 | 71 |
| 13 | 12.9 | 2 | 16 | 178 | 81 | 258 | 66 | 0 | 142 |
| 14 | 15.1 | 2 | 3 | 203 | 67 | 230 | 65 | 0 | 138 |
| 15 | 15.6 | 4 | 7 | 145 | 38 | 224 | 41 | 1 | 81 |
| 16 | 15.9 | 2 | 23 | 273 | 154 | 390 | 61 | 1 | 107 |
| 17 | 18.0 | 1 | 2 | 80 | 25 | 97 | 62 | 0 | 109 |
| 18 | 17.1 | 2 | 2 | 117 | 89 | 180 | 54 | 0 | 159 |
| 19 | 26.7 | 5 | 14 | 219 | 101 | 478 | 63 | 1 | 109 |
| 20 | 26.6 | 1 | 13 | 230 | 37 | 265 | 102 | 0 | 48 |
| 21 | 29.6 | 1 | 7 | 80 | 6 | 87 | 74 | 1 | 153 |
| 22 | 31.0 | 2 | 3 | 320 | 50 | 342 | 230 | 0 | 91 |
| 23 | 31.9 | 1 | 9 | 65 | 0 | 65 | 65 | 1 | 0 |
| 24 | 38.0 | 8 | 17 | 169 | 84 | 369 | 54 | 1 | 57 |
| 25 | 53.4 | 3 | 26 | 124 | 76 | 314 | 57 | 1 | 91 |
| 26 | 67.7 | 7 | 16 | 209 | 50 | 353 | 75 | 1 | 86 |
| 27 | 76.1 | 8 | 43 | 138 | 67 | 298 | 55 | 1 | 75 |
| 28 | 119.3 | 11 | 8 | 154 | 79 | 375 | 55 | 1 | 65 |
| 29 | 11.1 | 3 | 10 | 132 | 58 | 280 | 91 | 1 | 0 |
| 30 | 5.7 | 3 | 27 | 146 | 79 | 335 | 72 | 1 | 42 |
| 31 | 9.8 | 2 | 5 | 273 | 81 | 347 | 134 | 1 | 3 |

¹ This variable was transformed by LOG10 for analyses because of a skewed distribution.

² Presence (1) or absence (0) of wild and young trout.

stream fragments ranged from 0.4 km to 119.3 km in contiguous length with a median value of 15.1 km (data shown in Table 2). While all samples included some fish, most stream fragments had few species (median 2, maximum of 11). The density of fish per sample ranged from 2 to 51 with median of 16. The median length of fish collected by stream fragment was 169 mm with the central 50% ranging from 133 to 229 mm. The fish length maximums were commonly from 227 to 352 mm, and the middle 50% of the minimum lengths was 55 to 99 mm. The smallest fish recorded was 41 mm and the largest was 478;

both brown trout designated in the field notes as wild fish. The minimum elevation of the stream fragments ranged from 0 (sea level) to 185 m above sea level with a median elevation of 91 m.

The total number of fish collected in all stream fragment samples was 1109 including 22 species. Brown trout dominated (77%) the collections and more than half (58%) of these fish were stocked and greater than 152 mm total length (Table 1, scientific names shown). Brook trout were abundant in the samples and most were wild fish. The white sucker was equally abundant and generally large (highest median

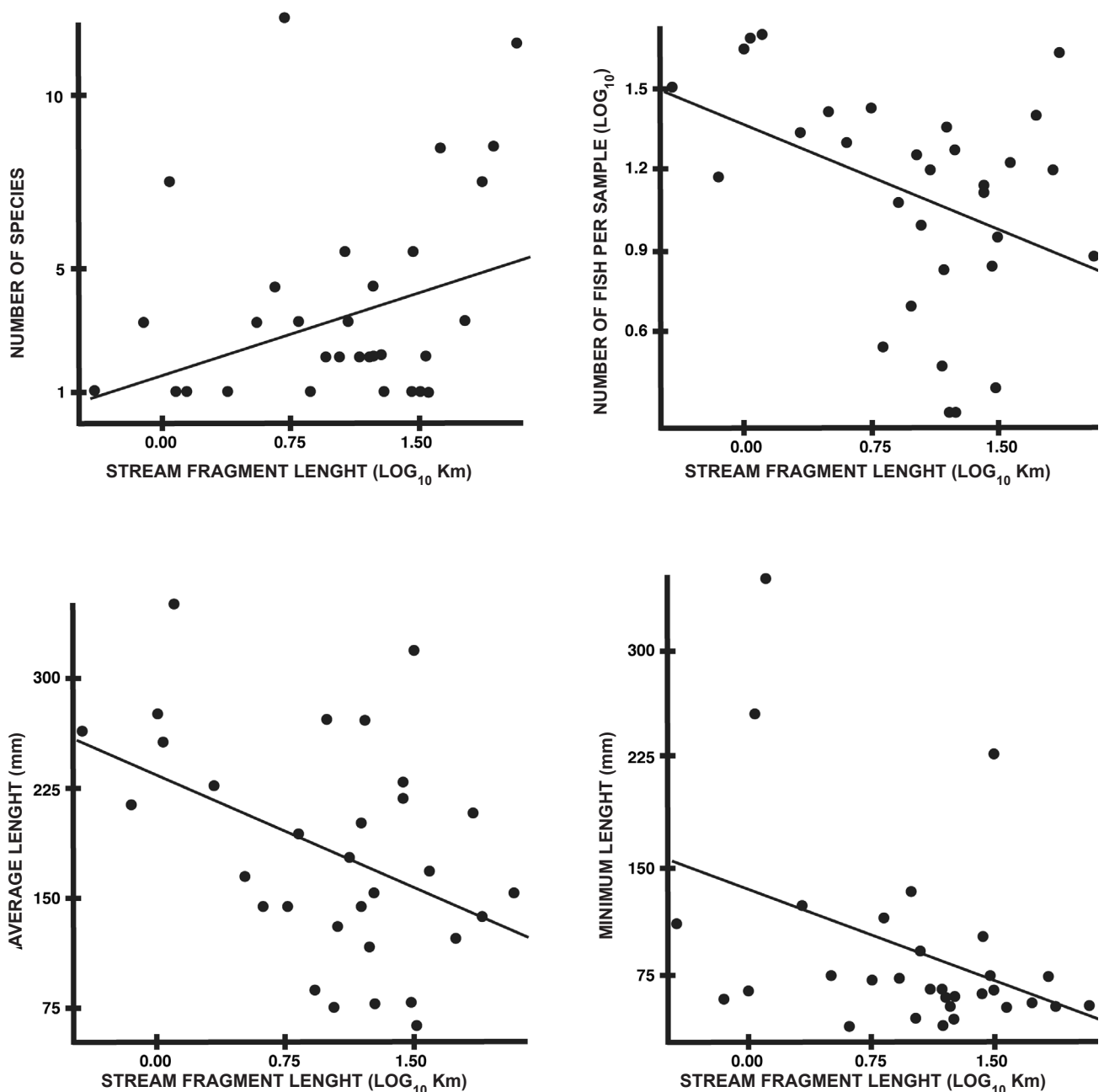


Fig. 1. Relations between stream fragment length and the number of fish species recorded, density of fish, average length of fish, and the minimum length of fish recorded.

length, Table 1). The rest of the species recorded were in relatively low numbers (Table 1) but were important to the diversity of fish in the collections. Three species (tessellated darter, eastern mudminnow, stocked rainbow trout) were very abundant or present in one or a few stream fragments. About a quarter of the species were not commonly recorded but added to the diversity of some sites.

The prediction that larger stream fragments have more diverse fish communities was supported by the data (Fig. 1). Stream fragment size was positively related ($P = 0.0295$) to the diversity (species counts) of fishes collected indicating that stream fragments with greater lengths support more species of fish. Long (≥ 40 km) stream fragments almost always had seven or more species while stream fragments less than 3 km in length mostly had one species recorded. Minimum elevation of the stream fragments was added to the regression model but was not a significant variable ($P = 0.2788$) and did not contribute to a better relationship between

opposite of what we predicted because large fragments had on average low fish densities. The highest density of fish recorded was in one of the shortest stream fragments (1.3 km) and other high density collections were in stream fragments less than 3 km in length. Minimum elevation of the stream fragments was not related to fish densities ($P = 0.7760$) nor was it a significant variable ($P = 0.4215$) in the regression model with fragment length.

The prediction that a wider range of fish sizes would be found in large stream fragments was not supported by the data. Both the range and standard deviation of fish lengths were not related to stream fragment length ($P = 0.3553$ and $P = 0.3544$ respectively). However, the average fish length per fragment was significantly related ($P = 0.0154$) to fragment length in an inverse manner (Fig. 1): short fragments have fish that were larger on average. This relationship was weak ($R^2 = 19\%$) because many relatively large stream fragments also had large average fish sizes.

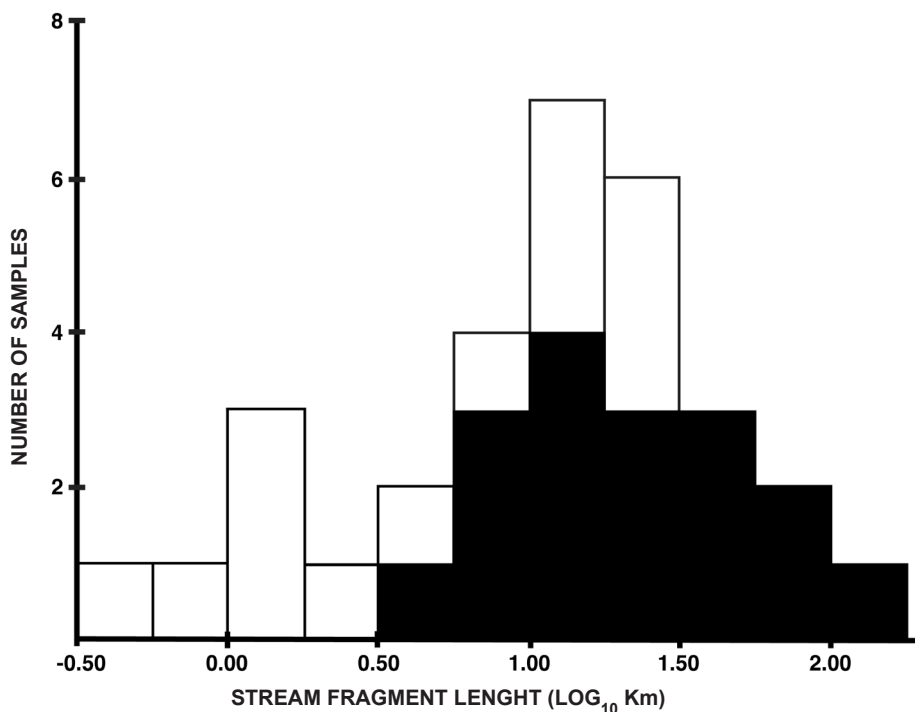


Fig. 2. Distribution of stream fragments supporting trout reproduction and yearling rearing (shaded) and those stream fragments not supporting wild trout production (unshaded).

fragment size and species diversity. Elevation was also not related to species diversity on its own ($P = 0.1490$). The prediction that fish densities would be related to stream fragment size was supported by the data and analyses (Fig. 1). There was a significant ($P = 0.0258$) relationship between fish abundance and stream fragment length. However, this relationship was

A regression test for a relationship with maximum fish lengths by stream fragment length indicated no relationship ($P = 0.7674$). However, the opposite test, with minimum fish lengths per fragment had a significant negative relationship ($P = 0.0340$) that was much more clear (Fig. 1). None of the long (≥ 40 km) stream fragments were limited to large fish while

many of the shortest fragments (< 3 km) had only relatively large fish (> 112 mm length). This result shows that the relationship between stream fragment length and the size distribution of fish resulted from a high abundance of small fish in large stream fragments. Again, minimum elevation of the stream fragments was not related to fish lengths ($P \geq 0.1332$) nor was it a significant variable with fragment length ($P \geq 0.1845$).

We grouped all stream fragments that were documented to have young trout (brown and brook) that were naturally produced and fragments without young trout. These stream fragments supporting wild and young trout were consistently and significantly larger (t-test, $P = 0.0013$). Almost all large stream fragments were shown to be supporting trout reproduction and rearing while small fragments had no evidence of providing this fish community support (Fig. 2). Large stream fragments generally included long sections of main stream channels and tributaries of varied sizes. Minimum elevation of stream fragments with wild and young trout were lower ($P = 0.0203$, median 77 m) than fragments lacking evidence of trout reproduction (median 118 m). Large stream fragments included main stream reaches at lower elevations connected to smaller tributaries reaching higher elevations.

Discussion

Of the three predictions tested, only the expectation that fish species numbers would increase with stream fragment length was supported by our analyses. Fish density and fish sizes were related to stream fragment length but opposite the hypothesized positive form. Lower fish densities and smaller fish were associated with large stream fragments. This pattern indicates that large stream fragments are supporting trout reproduction and rearing of young. Brown trout dominated the fish fauna of study streams and brook trout were very common. Both species were regularly stocked in the study watersheds. Stream fragments supporting young wild trout were consistently and significantly larger than the stream fragments without evidence of wild trout population support. This finding combined with a greater number of species in large stream fragments is consistent with the fundamental basis of stream landscape theory: large stream networks provide support for more species and more secure populations. Only large stream fragments supported reproducing populations of trout; the two species that comprise most of the fish recorded in the study watersheds.

Stocking of trout appears to have modified stream fish

populations which is the intent of this management practice. Many short, isolated stream fragments had only relatively large brown trout and often in high densities. These fish could have been restricted to short fragments by barriers and impounded downstream waters. In contrast, long stream fragments with tributaries would provide a range of habitats, allow greater fish dispersion, and harbor small young fish that resulted in lower average size and greater densities of young trout. Support for sustained trout populations in large stream fragments and trout stocking across all fragment sizes appears to have produced the pattern of results in this study. Our hypothesis was that relatively small stream fragments would have sparse fish populations dominated by small fish as reported by Letcher et al. (2007) for brook trout in the same US region. Unlike their study, it appears that in our streams the small isolated stream fragments had no reproduction, no juveniles, and were composed primarily of stocked trout. Similar findings were reported by Dunham et al. (1997) for trout in small isolated stream fragments in western USA streams. In that study, fish surveys recorded only relatively large fish and perhaps in elevated densities from stocking. In our heavily fragmented watersheds, redistribution of large fish and colonization of fragments by many species does not appear to be occurring as reported in other stream studies with many fewer barriers (e.g., Riley et al. 1992).

Coldwater trout dominated the fish fauna of our study watersheds, and thus stream position along the watershed continuum (e.g., Vannote et al. 1980) could have been expected to influence fish densities and successful reproduction. The minimum elevation of the stream fragments was not related to other variables in our regression models, nor was stream elevation related to other fish assemblage variables. Thus stream position and elevation does not appear important in this study where the watersheds were cool, well shaded streams throughout. Stream fragment elevation did differ for fragment groups with and without wild young trout. However, the fragments supporting reproduction had lower minimum elevations. This finding indicates that stream fragments supporting reproduction, young, and adult trout were composed of low elevation, relatively large streams connected to tributaries that included smaller streams and higher elevations. Thus a range of stream types and positions in the watershed appear needed to support the entire life cycle of trout.

Brown trout have been found to access different habitats in distant stream segments throughout

their life cycle. For example, Meyers et al. (1992) describe a clear case where large adults overwinter in deep habitats of the largest stream available, move upstream during the growing season, and reproduce in small head water streams. Only the larger stream fragments of our study watershed would support this life history pattern. Other cases of resident stream fish using a range of stream sizes and habitat conditions to complete their life cycle has been reported in other settings (Schlosser 1991, Harig et al. 2000, Harig & Fausch 2002), and is the basis for refuting the long held restricted movement paradigm for resident fishes (Gowan et al. 1994). Our findings are perhaps an extreme case of the benefit of connectivity in stream landscapes because of the long history of intense fragmentation in the study watersheds.

The use of routine agency fish survey data with detailed analysis of stream barriers yielded a clear picture of fish assemblage dispersion relative to stream fragmentation. In that sense, the regional scale agency data sets were adequate for this study. However many of our significant relations had considerable variability. It is also likely that fish sampling was biased to stocking areas and trout. This does not appear to be a major impediment because the species expected for streams in heavily forested areas of the Hudson River highlands were recorded. Also, the fish survey data and notes regularly documented

other fish species. The stream fragment identifications were in most cases verified by site visits, and our investigation of fragments using digital and map information reinforced the accuracy of these data.

Overall our findings support the concept that diverse fish communities and secure populations benefit from access to a wide range of stream habitats – the fundamental basis of stream landscape theory. Stream restorationists, watershed conservationists, and fishery managers should strive to reconnect stream reaches especially where a range of stream sizes and habitats are involved. While isolated stream fragments may support high concentrations of stocked trout, the capacity for streams to support secure wild populations appears consistent with the concept of providing a landscape or network of streams for fish fauna support.

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